Activity of the Gastropod Mollusk *Olivella biplicata* in Response to a Natural Light/Dark Cycle

BY

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(3 Text figures)

INTRODUCTION

Olivella biplicata (Sowerby, 1825) is a common snail on many sandy beaches along the west coast of North America from Baja California to Vancouver Island, British Columbia (KEEN, 1937). It is found both along exposed coastline and in protected bays and estuaries where it lives in relatively clean sands that contain minor amounts of silt and clay (STOHLER, 1969; EDWARDS, 1969b; JOHNSON, 1971). Its vertical range is from the extreme high of lower low water to the shallow subtidal area (EDWARDS, *op. cit.*). Previous studies on *O. biplicata* have dealt with reproduction and growth (STOHLER, 1959, 1960, 1962, 1969; EDWARDS, 1968; ZELL, 1955), predators (EDWARDS, 1969a), physiological tolerances (EDWARDS, 1969b), and the intertidal distribution of size classes (EDWARDS, 1969b).

In the present paper, a 24-hour activity cycle is reported for *Olivella biplicata*. The general activity cycle is described, activity patterns of individual snails are compared, and interrelationships between the size, sex, and activity of the snails are reported.

MATERIALS AND METHODS

Olivella biplicata were collected in the harbor at Bodega Bay, California. Specimens used in this study were collected intertidally on a sandy spit between the tidal levels of 0.0 and – 0.3 m. The *Olivella* population extended subtidally from this spit down to the bottom of the boat channel (– 6 m to – 7 m). After collection, the animals were maintained in aquaria provided with sand and a constant flow of seawater from the Bodega Marine Laboratory's running seawater system. Experiments were completed within 3 weeks of collection.

The observation chamber was a plexiglass trough (43 × 36 × 14 cm) containing a layer of sand 6 cm deep. The water level was 4 cm above the surface of the sand. Seawater from a constant-level reservoir entered the trough at one end through 4 inlet holes (13 mm diameter) and exited at the opposite end through 4 outlet holes (13 mm diameter). Water flow through the observation chamber was maintained at a rate of 2.5 *l*/min. Water temperature in the trough was usually 1 °C higher than ambient sea-surface temperature, which varied from 11.3 to 14.0° C during the experiments.

Individual *Olivella biplicata* were identified by writing a number on the shell with a felt-tipped marking pen (black, Color Pen, Perm-color, Esterbrook). All of the numbers remained clearly legible for over a week; however, after 2 weeks, the numbers were beginning to wear off. This marking technique would not be suitable for experiments of longer duration.

Observations at night were made with a flashlight fitted with a red filter (Kodak No. 29, dominant wavelength of 633 nm). In addition to the red filter, 4 sheets of Whatman No. 1 filter paper were placed in the light path to reduce the intensity of illumination and to provide a more uniform light source. The flashlight was powered by 2 standard, "D" batteries (1.5 v each).

RESULTS

General Activity Patterns

Fifty-seven individually numbered *Olivella biplicata* (hereafter *Olivella*) were observed in a large plexiglass chamber, which contained a layer of sand and was provided with running seawater. The observation chamber was located outdoors under an overhang that sheltered the chamber from direct sunlight except during late morning hours. In this location, the animals were exposed to a light/dark cycle that was similar to the natural cycle but with light that was somewhat reduced in intensity. During mid-August (when this experiment was conducted) the animals were exposed to light (> 10 footcandles ≈ 108 lumen per m^2) from approximately 06:15 to 20:15 (Pacific Daylight Time).

After a 24-hour acclimation period in the observation chamber, the snails were observed every hour for 5 days. Since active snails were almost always on the surface of the sand and buried snails rarely moved, the number of snails on the surface was used to quantify the activity of the *Olivella* population. Figure 1 is a summary of the numbers of *Olivella* recorded on the surface at one-hour intervals during the 5 days.

The most striking feature shown by Figure 1 is that the *Olivella* were on the surface and active primarily at night. Fully 88% of the observations of animals on the surface were recorded during the hours of darkness (21:00 through 06:00). Consistently, the number of animals on the surface began to increase at twilight and rapidly reached a maximum, usually within 2 hours of darkness. Similarly, each night the number of animals began to decrease long before the light of dawn. While activity was clearly greatest during the night, it should be noted that some activity was also recorded during each 14-hour daylight period.

Since the numbers of *Olivella* on the surface began to decrease well before dawn and to increase somewhat before complete darkness, it was desirable to directly test the snails' responses to light and to dark. One hundred *Olivella*, which had been in the observation chamber for the 2 previous days, were exposed to complete darkness at 14:00 by covering the chamber with aluminum foil. Two hours later, the cover was removed exposing the animals to ambient, late afternoon lighting conditions (90 footcandles, ≈ 972 lumens per m^2). The results of this experiment are reported in Table 1. It can be seen from Table 1 that before darkening the chamber only 1 of the 100 *Olivella* was on the surface. However, after 2 hours of darkness artificially imposed during the day, 53 of the *Olivella* had emerged and were on the surface. Re-exposure to daylight produced an immediate burial response. Within 2 minutes, over half of the animals had completely buried themselves, and, within 8 minutes, all of them had disappeared under the sand. Light, and the absence of light, clearly has a direct influence on the activity of *Olivella*.

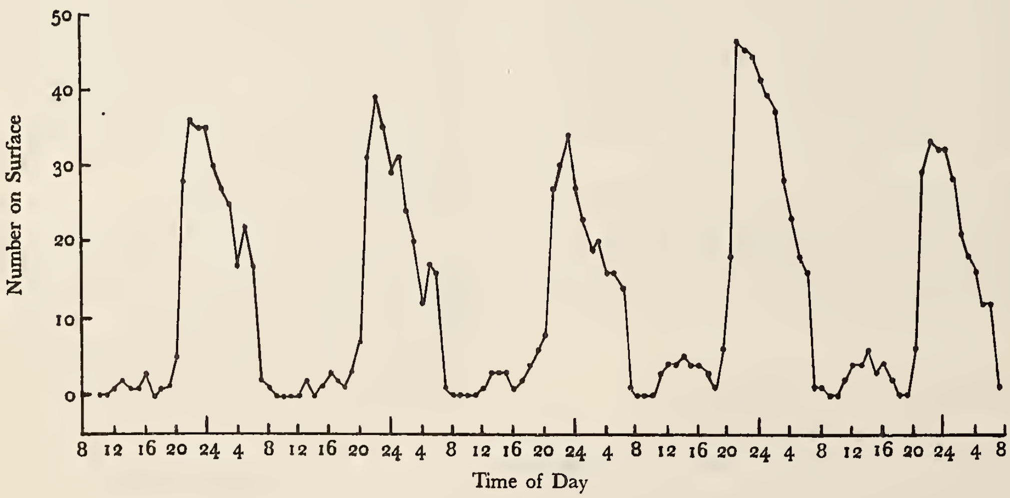

Figure 1

Numbers of *Olivella biplicata* on the surface (N = 57) at 1-hour intervals through 5 complete light/dark cycles. Snails were maintained outdoors and were exposed to daylight (> 100 Lux or > 10 footcandles) from approximately 06:15 to 20:15 (Pacific Daylight Time). A snail was recorded as being on the surface if ⅔ or more of its shell length was visible.

Table 1

Responses of *Olivella biplicata* to darkness artificially imposed during the day (N = 100), and responses of snails on the surface to daylight (90 footcandles)

Operation	Time	Number on Surface
Chamber darkened	14:00	1
Chamber exposed to daylight	16:00	53
	16:02	20
	16:04	8
	16:06	3
	16:08	0
	16:10	0
	16:20	0

Activity Patterns of Individuals

The general activity pattern of the *Olivella* population (Figure 1) was relatively constant from one 24-hour period to the next. In contrast, the activity patterns of individual snails were extremely variable, and the records of 10 individual *Olivella* are presented in Figure 2 to illustrate this diversity. The median number of times that a snail was recorded on the surface during the 120 hours of observation was 24 times. The activities of many individuals, however, varied widely from this median value. For example, snail #7 was recorded on the surface 53 times (*i. e.*, during almost half of the observations), whereas snail #56 was observed on the surface a total of only 3 times during the 5 days. The percentage of an individual's activity that occurred in the dark or in the light was also variable. Although most of the snails were active primarily or exclusively at night (*e.g.*, snails #10, 23, 25, 29, 32, 46, and 56), several of the snails had activity patterns that were characterized by substantial percentages of daytime activity (*e. g.*, snails #7, 28, and 31). Even among the snails that were active primarily at night, the specifics of the activity patterns varied considerably from individual to individual. For example, snail #29 was not seen on the surface at any time during 2 of the 5 nights of observation, but it was very active during the other 3 nights. In contrast, snail #46 was out on the surface every night, but it stayed out each night for only a short time. All of the *Olivella* were observed on the surface at some time during the 5 days.

While observations at 1-hour intervals gave an adequate picture of an individual's general activity cycle, an hour was a long time compared to the time actually needed for an *Olivella* to bury itself and re-emerge. Was it likely that an animal observed on the surface at 22:00 and again at 23:00 had spent the entire hour on the surface? Or had it perhaps buried itself and re-emerged several times during the hour? To answer these questions,

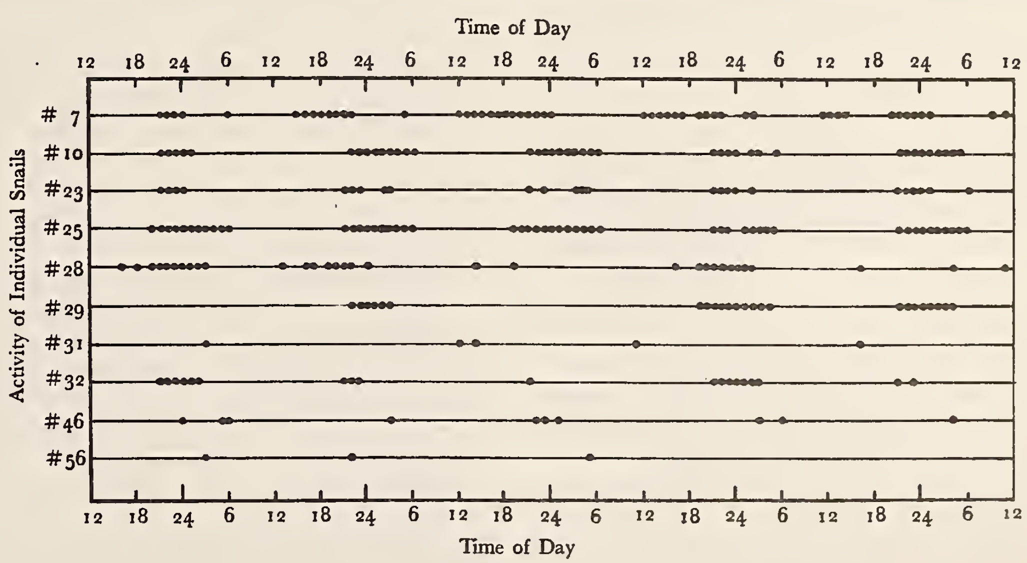

Figure 2

Activity records of 10 *Olivella biplicata* selected to illustrate the diversity of individual activity patterns. Observations were made at 1-hour intervals for 5 complete light/dark cycles. Darkened circles indicate the times that each individual was observed on the surface.

the 57 numbered *Olivella* were observed continuously for one hour (23:00 to 24:00) with data being recorded every 5 minutes. The results were clear. Of the 23 individuals that were on the surface both at the beginning of the observation period (t = 0 min.) and at the end (t = 60 min.), 20 were on the surface for the entire hour. Of the 35 individuals that appeared on the surface at least once during the hour, only 3 individuals were observed on the surface, then not seen, and later observed again on the surface; furthermore, 2 of these 3 were not seen for only 1 observation, suggesting that they might have been on the surface but overlooked. Almost all of the snails that were observed on the surface were active and moving.

In addition to showing that an individual observed on the surface for 2 consecutive hourly observations was likely to have been on the surface throughout the hour, these short-interval observations provided an important control for possible effects of the red light used to make all of the observations. Table 2 reports the total numbers of *Olivella* on the surface at 5-minute intervals during the hour of observations. There was no significant difference between the numbers of *Olivella* on the surface at the beginning and at the end of the hour ($x^2 = 0.32$; $p > 0.5$). A slight decrease was observed; however, this decline was consistent with the general activity cycle of *Olivella* (Figure 1) in which activity often appeared to decline between 23:00 and 24:00. If there was a response to the red light, it was clearly unlike the strong burial response to daylight that was reported in Table 1. While it is never possible to completely prove "no effect," the conclusion appears justified that the red light did not significantly affect the basic activity pattern of *Olivella*.

Table 2

Numbers of *Olivella biplicata* (N = 57) on the surface recorded at 5-minute intervals during one hour of continuous observation (23:00 to 24:00)

Time (Min. after 23:00)	Number of snails on surface
0	31
5	31
10	31
15	32
20	32
25	33
30	30
35	31
40	30
45	29
50	29
55	27
60	27

Relationships Between Shell Length, Sex, and Activity

Olivella were collected for the preceding experiments without regard to sex or shell length. After the experiments, individuals were measured and sexed. Shell length (apex to siphonal canal) was determined with vernier calipers. The lengths ranged from 18.2 to 27.9 mm ($\overline{X} = 22.7$; SD = 2.4). Sex was determined by using the presence or absence of a penis as the test criterion. Using this criterion, the sample of 57 *Olivella* contained 38 females and 19 males. Eleven of the males had functional penes; 8 had rudimentary penes, probably resulting from trematode infections. All animals designated as females were examined under the dissecting microscope to make certain that a penis rudiment had not been overlooked. The total number of times an individual was observed on the surface was taken as a relative measure of its overall activity. These relative activity measures ranged from 3 to 57 times on the surface during the 5-day experiment ($\overline{X} = 25.4$; SD = 12.4).

In Figure 3, shell lengths were plotted against the number of times a snail was observed on the surface (*i. e.*, activity). Small snails were generally more active, and activity gradually decreased with increasing shell length. The negative correlation between shell length and activity was highly significant when both males and females were included in the analysis (corr. coeff. = − 0.52; d. f. = 55; $p < 0.001$). A significant correlation was also present when females were considered alone (corr. coeff. = −0.39; d. f. = 36; $p < 0.05$). A significant correlation was not present between shell length and activity when only males were considered (corr. coeff. = + 0.03; d. f. = 17; $p > 0.5$). The sample linear regression for all of the data (males plus females) was expressed by the equation $Y = 25.2 - 0.1X$.

Males and females were plotted with different symbols in Figure 3, and it was immediately apparent that males in this sample were considerably larger than females. Males had shell lengths averaging 25.3 mm (N = 19; SD = 1.5), whereas the average shell length of a female was 21.4 mm (N = 38; SD = 1.5). The difference between the sample means was highly significant (t-test; $p < 0.001$).

Since females were generally smaller than males, and since smaller snails were more active, it was expected that females would be more active than males. This was true. Females were observed on the surface an average of 29.5 times during the 5 days (SD = 11.6) compared to only 17.0 times (SD = 8.9) for males. The difference between

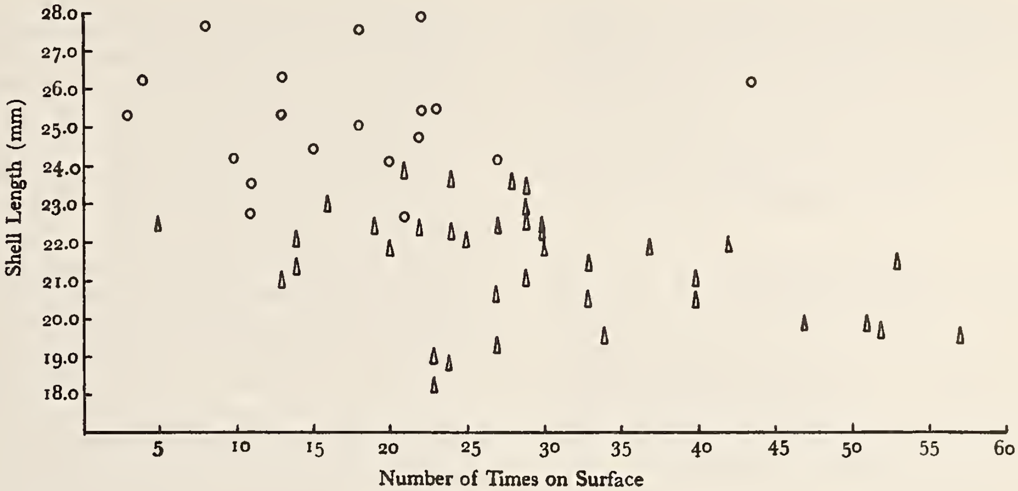

Figure 3

Relationship between shell length and the total number of times a snail was observed on the surface during the 5-day experiment (*i. e.*, activity). Males (○) and females (△) are indicated separately. The correlation is significantly negative when both males and females are included in the analysis (corr. coeff. = −0.52; d. f. = 55; $p < 0.001$). The sample linear regression is expressed by Y = 25.2–0.1X.

the sample means was again highly significant (t-test; $p < 0.001$). Females tended to be more active both during the day and during the night. This difference was highly significant during the night (t-test; $p < 0.001$). Few individuals were active during the day, however, and the difference in daylight activity between males and females was not statistically significant (Mann-Whitney U test; $p < 0.2$).

While the activities of males and females were clearly different, it was not possible with these data to assess satisfactorily the contribution of sex independently from size effects. There was so little overlap between the size distributions of the 2 sexes (Figure 3) that few males and females of similar size were available for direct comparisons. There was some overlap in size, however, between the 6 smallest and 7 largest females (22.6 to 24.2 mm). When the activities of these 13 animals were compared, females were again found to be more active than males (Mann-Whitney U test; $p < 0.05$).

Although *Olivella* were collected for this study without regard to sex, the sample contained many more females than males. Indeed, the numbers of males and females were significantly different from the 1 : 1 ratio that was expected on the basis of previous work (Edwards, 1968). While this deviation was statistically significant ($X^2 = 6.63$; $p < 0.025$), it may have resulted completely from unintentionally biased sampling related to activity differences between the sexes. Many of the *Olivella* used in this study were collected from the surface of the sand. If it can be assumed that females are generally more active (*i. e.*, spend more time on the surface) than males, then a sample of animals taken from the surface should contain a larger proportion of females than is actually present in the total population.

Field Observations

While a comprehensive field study of *Olivella biplicata*'s activity cycle was not undertaken, numerous trips to the field have provided opportunities to qualitatively confirm the activity cycle. Most of these observations, taken at various times during the day and night, were made at the collecting site, a sandy spit in Bodega Harbor. *Olivella* were observed at this intertidal site during low water when they were still covered by 10 to 50 cm of water. In addition, a few observations were made on subtidal *Olivella* along the bottom of the nearby boat channel (6 to 7 m deep). The *Olivella* population in this channel appears to be continuous with the intertidal population. Both intertidal and subtidal observations confirmed the activity cycle that was seen in the laboratory: many *Olivella* were active on the surface of the sand during the night; few were active during the day.

DISCUSSION

Olivella biplicata maintained under natural lighting conditions were active primarily at night. Most of the snails remained buried in the sand throughout the day, occasionally moving beneath the surface for short distances. At twilight snails began to emerge from the sand, and, within 2 hours, large numbers were moving across the surface. Direct responses were given to light and to dark (Table 1), but *Olivella* also appeared to anticipate changes in the natural lighting cycle (Figure 1): the numbers of animals on the surface always began to increase sometime before dark and always began to fall several hours before dawn. This anticipation suggests the possibility of an endogenous circadian rhythm. Field observations confirmed the general activity cycle. Few snails were seen on the surface during the day, whereas hundreds were seen during the night. Similar field observations have been made by other investigators (Edwards, 1969b; Van Veldhuizen, personal communication).

The nocturnal habit of *Olivella biplicata* may be an evolutionary response to the threat of visual predators. *Olivella biplicata* is a slow-growing animal with a low recruitment and an estimated life-span of greater than 10 years (Stohler, 1962, 1969; Edwards, 1968, 1969a). With a reproductive strategy of this sort, efficient and effective means of avoiding potential predators would appear to be important. Gulls and other shore birds occasionally prey upon *Olivella* species during low tide (Cottam, 1939; Grinnell, Bryant & Storer, 1918; Martin & Uhler, 1939; Edwards, 1969a; Reeder, 1951; Stohler, 1969). Fish are also known to consume these snails (Iverson, 1972; Turner, Ebert & Given, 1969). The numbers of *O. biplicata* actually taken by these visual predators would appear to be very small, however, since adult *O. biplicata* have excellent survivorship (Edwards, 1969).

While the general activity cycle of the *Olivella* population was relatively well-defined and predictable, the activity patterns of the individuals that made up the population were quite variable. A portion of this variability was related to differences in size and sex. Male *Olivella* in this sample were considerably larger than females: males ranged in shell length from 22.7 to 27.9mm, whereas females ranged from 18.2 to 23.9mm. This supports earlier findings (Edwards, 1968, 1969b) that male *Olivella biplicata* grow faster and attain larger maximum sizes than do females. Since both sexes of *O. biplicata* have been reported to mature sexually at a shell length of 16 mm (Edwards, 1968), all of the snails in this sample were of sufficient size to be considered sexually mature.

In the present study, smaller *Olivella* (mostly females) spent more time on the surface and were more active than larger snails (mostly males), and this was true both during the day and during the night. These results are opposite to the results reported by Edwards (1969b); his general conclusion was that large *Olivella* were more active than smaller *Olivella*. Some of the apparent contradiction may be related to differences in the emphasis placed on daytime and nighttime activity in the two studies and also to different lighting conditions. Edwards (*op. cit.*) emphasized activity taking place during daylight hours; in contrast, the present study emphasized the light/dark cycle of activity, and consequently, activity taking place at night. Edwards' experiments were also conducted indoors with lighting provided by a nearby window. He reported that for a short time each morning, the animals were exposed to direct sunlight through this window, and for the rest of the day, they were in shadow. Considering the day as a whole, he concluded that large snails were generally more active than small snails; he added, however, that during the short exposure to direct sunlight, smaller animals were more active and were found more often on the surface than were larger snails. Edwards' results in bright light are in agreement with the conclusions of the present study, which was conducted under relatively bright, outdoor conditions.

While the present study on *Olivella* concentrated specifically on the behavioral effects of a light/dark cycle, many factors in addition to light clearly influence this snail's activity. For intertidal snails, the tidal cycle is probably the most important of these. *Olivella* which are exposed by the receding tide immediately bury themselves in the sand (Stohler, 1969); they remain dormant until the water returns, regardless of the time of day or night (Phillips, unpubl. data). Stohler (*op. cit.*) also reports that similar responses to tidal conditions may occur even when the animals remain covered by several decimeters of water. The presence of food also influences activity; if a piece of crab or mussel meat is placed on the surface of the sand during the day, many of the buried *Olivella* will suddenly emerge and begin searching for the food (Phillips, unpubl. data). Mating condition may influence activity; sometimes during experiments, a male would emerge from the sand to begin courting a particular female that passed by on the surface. Many more factors, such as the amount of turbulence and the presence of potential predators, are probably also important. So, while the light/dark cycle clearly exerts a major influence on the behavior of *Olivella*, the activity patterns of this snail are complex and intricately related to a variety of factors.

SUMMARY

1. The activities of individually marked *Olivella biplicata* were monitored every hour for 5 complete light/dark cycles. The animals were maintained in a plexiglass trough that was supplied with running seawater and located outdoors.
2. The *Olivella* were active primarily at night. During the day, most of the snails remained buried in the sand and rarely moved; at twilight, they began to emerge from the sand, and, within 2 hours of darkness, maximum numbers of snails were active on the surface.
3. While the general activity cycle of the *Olivella* population was well-defined and predictable, the activity patterns of the individuals that made up the population were quite variable. A portion of this variability was related to differences in size and sex.
4. Females in this sample were considerably smaller than males (t-test; $p < 0.001$).
5. Small snails were generally more active than large snails (correlation coefficient $= -0.52$; d.f. $= 55$; $p < 0.001$).
6. Females were more active than males (t-test; $p < 0.001$).
7. Field observations during the day and night confirmed the existence of *Olivella*'s activity cycle.

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